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Introduction

This is an account of a mathematical simulation model of the behaviour of plankton populations in space and time. The main aim of the model is to study the formation and persistence of plankton patches. In particular, we investigated the idea that much of the horizontal variability of plankton is the result of vertical processes like turbulent mixing and zooplankton migration.

Sverdrup (1953) showed that the formation of a spring thermocline is critical in triggering the phytoplankton bloom by trapping a few plant cells in a region of high illumination. Since the thermocline may not form everywhere at the same depth or the same time, we expect spatial variations of phytoplankton concentrations to occur during the outburst period.

Assuming that a patch existed, several people, beginning with Skellam (1951) and Kierstead and Slobodkin (1953), considered the problem of maintaining it against horizontal mixing. Much of the observed horizontal mixing in the sea is believed to be the result of vertical mixing interacting with vertical shear in horizontal currents (Bowles, Burns, Hudswell and Whipple, 1958; Okubo, 1967; Kullenberg, 1974). If this is true, it should have an important effect on the plankton, for while they may be supposed to drift passively with the water horizontally, animals (and to a lesser extent plants) have definite motions through the water vertically. Such motions imply that horizontal dispersion rates will be different for nutrients, plants and animals. Kamykowski (1974, 1976) and Riley (1976) have looked at aspects of this process.

We modelled one horizontal dimension at four depths, looking at the dynamics of one dissolved nutrient, one species of phytoplankton, and one of herbivorous zooplankton. Since herbivore migration plays an important part in the model, and since migratory behaviour changes greatly with age, we divided the herbivores into three size classes corresponding to different stages in the life history.

This is a preliminary model, and it ignores several things which we know are important. In particular, it is restricted to biological patch-generating processes: physical processes like vertical mixing are horizontally homogeneous in this model. Our ultimate goal is a model in which the currents and mixing rates are calculated from wind and heat input, and can vary in time and space.

Modelling

Physics

The physical picture is of a two-dimensional sheet of water in a vertical plane. The sheet has finite horizontal extent, and is divided vertically into

four layers of finite thickness. The two lower layers are fixed, the upper two move independently as rigid bodies with predetermined combinations of steady and oscillating velocities. There is no horizontal diffusion, but vertically adjacent layers are mixed, and therefore exchange nutrient and phytoplankton (but not herbivores – see later). The rate of exchange for a given interface is constant, independent of time and horizontal position.

Because of the finite horizontal extent, we must assign boundary values to the various concentrations. There are three obvious possibilities, as follows.

(1) Pre-set boundary values. These could be constant or varying in some manner determined from theoretical considerations, a programme of observations, or runs of the model without advection. The major drawback is that the evolution of the model would probably be driven largely by the boundary values selected. If we are looking for patches, departures from the mean, it is unsatisfactory to have the ends of the system constrained to some average behaviour. Another difficulty relates to the oscillating currents; concentrations near the downstream end might evolve away from the downstream boundary conditions, and therefore a discontinuity would arise when the current reversed.

(2) Flat or reflecting boundaries. The concentrations just outside the boundary are deemed to be the same as those just inside, so that there is no net exchange. This would be appropriate to a physical situation with real reflecting boundaries like coasts, but it is not as good for the open sea, especially since flat boundaries tend to damp out variations.

(3) Circular boundary. This essentially means no boundary; each layer is considered to be tied together in a ring, so that the model evolves with no outside interference. Although the solution is constrained to have a definite spatial period, this should not be a great problem, since the period can be chosen differently in different runs. The physical situation pictured is not unknown, eg gyres or Gulf Stream rings. Note that a strip of length L with flat boundaries is a special case of a ring with circumference 2L.

In order to model a region with uniform velocity and a fairly precise, fairly constant upstream boundary, like a plume downstream from an upwelling area, (1) would be the proper choice. Our interest is more in open homogeneous seas, so we have used (3). This choice would be difficult to extend to three dimensions.

Biology

We express the dissolved nutrient N, the phytoplankton P, and the herbivores H in a common unit. We assume that the limiting nutrient is nitrogen in the form of nitrate and/or ammonia, and write equations for its transfer among the three forms:

$$\frac{dN}{dt} = \text{(net production)} + \text{(soluble herbivore excretion)}$$

$$\frac{dP}{dt} = \text{(net production)} - \text{(herbivore grazing)}$$

$$\frac{dH}{dt} = \text{(net ingestion)} \quad - \text{(predation)}$$

These equations describe events within a well-mixed system; transfers between adjacent regions will be dealt with later, as will herbivore size structure.

$$\text{Net production} = \frac{a\ N}{b + N}\ P - c\ P \qquad (1)$$

The first term, gross production, depends on the supply of nutrient, with a hyperbolic saturation curve (Dugdale, 1977). The second term is cell respiration. The parameters a, b and c are constant in the model. In nature, a at least depends on light and heat, so the model can be run only for periods when these are considered constant.

$$\text{Herbivore grazing} = \frac{d\,(P - P_o)}{e + P - P_o}\ H \qquad (2)$$

This term, also, is hyperbolic above a threshold concentration P_o, below which no grazing occurs. The existence of this threshold is still subject to speculation (Steele and Frost, 1977). A constant fraction of the food grazed is assimilated for growth, and another constant fraction is excreted and becomes dissolved nutrient. The rest becomes faecal pellets which drop out of the system.

Predation on the herbivores is a constant fraction of their numbers. Since we decided not to model the population of carnivores, any predation term must be a compromise and this is the simplest one. However, there is a case for saying that predation should rise more slowly than H - if the predators are mostly a constant and satiable population of fish. There is also a case for saying it should rise more quickly - if the predators are mostly insatiable jellyfish whose numbers can rise rapidly in a good food supply. Several authors (Segel and Jackson, 1972; Landry 1976; Steele, 1976) have shown that the form of the predation term can have an important effect on model behaviour. We intend to investigate the effect of more general forms of predation in a later version of this model.

The subdivision of herbivores into three size classes means that the assimilated food of, say, nauplii is not used for increasing the nauplius biomass, but rather for turning a few nauplii into copepodites. We assign fixed weights W_1 and W_2 to the typical nauplius and copepodite respectively, so that each nauplius must gain an amount of weight $W_2 - W_1$ to become a copepodite. Then if the total net ingestion of all the nauplii is E, we assume that it is used to add a weight $(W_2 - W_1)$ to each of $E/(W_2 - W_1)$ nauplii and turn them into copepodites. This increases the number of copepodites and decreases the number of nauplii. For adults, we say that the net ingestion goes to produce E/W_1 nauplii, without any loss of adults.

This approach has its problems, since a just-promoted nauplius is at once eligible for promotion to adult, whereas in nature this would take at least ten days. The effect is to smooth out variations in herbivore size structure. However, we feel the difference in migratory behaviour is important enough to preserve size structure in the model.

As well as being carried around by the water, plankton has some extra vertical motions. Plant cells tend to sink, at a rate which increases as they stop growing (Eppley, Holmes and Strickland, 1967). We use the formula

$$\text{Phytoplankton sinking velocity} = V_{max}\,(1 - \frac{N}{b+N})$$

where V_{max} is the maximum sinking rate and $\frac{N}{b+N}$ comes from (1).

Diurnal vertical migration by herbivorous copepods is an established phenomenon which is mainly determined by light (Longhurst, 1976). Other factors, however, may alter the vertical movements. Conover (1968) discussed the possible consequences of satiation while feeding at night in the upper layers. Adult animals may fill their guts more quickly than they can digest. If this happens, they could stop feeding and descend to deeper

layers while it is still dark. This seems to have been confirmed by Pearre (1973) for carnivores (*Sagitta*), and by Mackas and Bohrer (1976) for copepods. There is also evidence (Raymont, 1963) that the nauplii remain in the upper layer and the pre-adult copepodite stages may have less vertical migration than the adults. Thus these three size categories are given different migration patterns.

We then look at the following model of migration, for one size class; the model is the same for all three, although the numbers will be different. At noon, all the animals are in the bottom layer. At some pre-set time they all rise, and must choose which of the upper three layers to rise into. They do this according to the attraction of each layer and divide their concentrations in proportion to the attractions. The attraction of a layer has two components: the mere fact of its existence and the availability of food, expressed as $\frac{P - P_o}{e + P - P_o}$ from (2). The ratio of these two components is a constant to be specified for each class, as is the time of ascent. Each class must also have specified a time of descent and a daily ration. When the ration has been filled or at the descent time, whichever comes first, the animals descend again, and promotion takes place on the way down. Herbivores are not affected by vertical mixing; we assume they can swim well enough to maintain their desired position in the water column.

Note that the bottom layer serves only as a reservoir for animals and a constant source of nutrients. No biological reactions occur there, and any phytoplankton mixed or sinking into this layer is lost to the system. The system is kept from running down by nutrients mixed up from this reservoir.

Numerical methods

As a first approximation, we want to solve a system of partial differential equations of the form

$$\frac{\partial \mathbf{B}}{\partial t} + \frac{v\, \partial \mathbf{B}}{\partial^x} = \text{Biol}\,(\mathbf{B})$$

where Biol is an operator standing for all the biological and vertical interactions going on. However, that is only a first approximation. **B** is a 15 - component vector, 5 components on each of three active levels. v is not a constant or even just a function of time; it varies between levels. Not all the changes are continuous; the migrations take place instantly. (This is perhaps a weakness of the model, since there is always some spread in timing.) Partly for these reasons, and partly because the concepts in the model are always changing, we feel that the numerical techniques should be kept as simple as possible, whatever the cost in computing time and accuracy.

We use the following principle in evaluating numerical techniques. No numerical method will give an exact solution to our problem. However, any numerical method will give an exact solution (apart from rounding errors) to some problem, and it is usually easy to identify what this problem is. If we feel it is acceptably close to ours, remembering all the approximations we have made already, then the method is acceptable.

Because of the discontinuities in migration, we use forward differencing in time:

$$\mathbf{B}\,(t + \Delta t) = \mathbf{B}\,(t) + \Delta t \quad \mathbf{B}'\,(t)$$

We have to divide the horizontal dimension into discrete cells, and here we use a non-standard method. Instead of considering the cells to be fixed in space, we consider them to be fixed in the water, rotating with the rings. This means that we have no horizontal transfers between cells. This could

be thought of as a Lagrangian approach to numerical fluid flow, and it avoids the familiar problems of finite difference methods in the Eulerian approach with cells fixed in space. A result of this is that cells do not usually line up vertically, and so vertical exchanges are more complicated.

Exploration of the Model

The investigations we have performed so far fall into three classes. First there are what might be called the dye runs, in which all the biological rates are set to zero so that phytoplankton and nutrients can be regarded as passive contaminants like rhodamine dye. These runs can be compared with theories and experiments involving dye mixing. Secondly, there are the column runs, in which the horizontal direction is suppressed. These runs will describe the behaviour of the model in a homogeneous sea, and provide a reference point for looking at spatial variation later on. Thirdly there are the full runs, with shear and biology. These have so far tended to be exploratory rather than systematic - the number of possible runs and the amount of output which a run can produce are both overwhelming. Some work has been done on the use of spectral theory to summarise results - this may also be a useful tool for comparison with observations (Platt and Denman, 1975).

Units and typical values

This section gives a feel for the units and an idea of the numbers that are commonly used.

Layer thicknesses : upper two 10 m each
third 20 m

We do not need a thickness for the fourth layer — within the model nothing happens there, so we are not interested in changing concentrations.

Mixing rates = between first and second $5\ m^2 h^{-1}$
between (second and third) / (third and fourth) $0.1\ m^2 h^{-1}$

($1\ m^2 h^{-1} = 2.78\ cm^2\ s^{-1}$)

Each of the two horizontal velocities is made up of a steady component and nine oscillating components with periods 6¼, 12½, 25, ... 1600 hours: all ten amplitudes must be read in for both of the upper layers. (1600 hours ≈ 2 months). Values vary widely: from 0.05 to 1 km h^{-1}. One common choice is a 12½ hour oscillation with maximum velocity 0.8 km h^{-1} in the top layer and 0.4 in the mid. (The layers are often called top, mid, bottom and deep. The unit of distance is the metre vertically, and the kilometre horizontally. The unit of time is always the hour.)

The concentrations of dissolved nutrients and phytoplankton are measured in millimoles of nitrogen per cubic metre (mM N m^{-3}), which is the same as μM N 1^{-1}. The concentrations of animals are measured in thousands per m^3 (ie numbers per 1) or vertically integrated as thousands under a sq. m. If a carbon:nitrogen ratio of 7 is assumed for plants and animals, then, approximately 1 mM N = 100 mg C.

Maximum photosynthetic rate, measured in h^{-1} (ie fractions of plant weight per hour), is a function of depth since the sunlight is attenuated at depth. We have used values of 0.01 - 0.03 for the top layer, 0.005 - 0 for the bottom. A rate of 0.01 corresponds to a doubling time of about 3 days. It might be more realistic to use a single maximum photosynthetic rate for ideal light and nutrient conditions, and model light attenuation explicitly, perhaps including the effects of plant self-shading. However, as always, increased realism implies increased complication, which might decrease overall understanding.

Half-saturation constant (b in equation (1)) is typically 1 mM N m^{-3}. This is the concentration of nutrient at which primary production is half its maximum rate.

Plant respiration rate 0.002 h^{-1} (0.05 day^{-1})

Animal weights: nauplius 0.01 μM N
copepodite 0.1
adult 1.0

Multiplying weight in μM N by numbers in thousands per m^3 gives nitrogen concentration in mM N m^{-3}, the same as nutrients and plants.

Maximum grazing rate, in μM N h^{-1} per animal
nauplius 0.001
copepodite 0.005 - 0.01
adult 0.025 - 0.1

The spread in copepodite and adult rates comes from uncertainty about whether grazing should be proportional to body weight to the power 1 or $\frac{2}{3}$ Total ingestion probably has a $\frac{2}{3}$ power relation, but this might be a result of satiation rather than of maximum instantaneous rate (Conover, 1968). The maximum rates, if maintained for 24 hours, would mean eating 2½ times body weight.

Daily ration, in μM N
nauplius 0.03
copepodite 0.05 - 0.13
adult 0.1 - 0.7

The higher values are perhaps more likely. They correspond to 3, 1.3 and 0.7 times body weight respectively.

Grazing threshold 0.25 - 0.5 mM N m^{-3} for all size classes.

Grazing half-saturation constant 0.5 - 1 mM N m^{-3} for all size classes.

Fraction of grazed material used in growth: 0.3 for all classes, or sometimes reduced to 0.15 for adults to simulate 50% egg mortality.

Fraction of grazed material going to soluble excretion: 0.3

Predation rate: 0.001 - 0.005 h^{-1}

Maximum plant sinking rate: 0.08 m h^{-1}

Nutrient concentration in deep water: 10 mM N m^{-3}

Migration parameters: Nauplii typically spend all their time in the active layers, copepodites 16 hours per day, and adults 12, though satiation may reduce this. The attraction of a layer has the form

$$ZMA + (1 - ZMA)\ (food)\ ;$$

we usually take ZMA = 0.5

Initial conditions for pre-outburst

nutrients 10 mM N m^{-3}
phytoplankton 0.5
nauplii, copepodites 0
adults 2 animals/l (2000 m^{-3})

Dye runs

We performed a series of runs in which the biological reaction rates are zero, so that the nutrients and phytoplankton are passive contaminants. These runs then simulate the spreading of a patch of dye.

The results of dye mixing experiments are generally presented as the variance in the position of dye particles, ie the mean square distance of a particle from the centre of the patch (Okubo, 1971). The rate of increase of horizontal variance with time is a measure of the horizontal diffusion rate. (We are dealing here with variance in position. In later spectral work we refer instead to variance in concentration.) These dye runs were therefore designed to calculate the variance in position of nutrients, phytoplankton and adults.

An exact solution for one special case, mixing only across one interface, steady shear across this interface (Evans, 1977), provides an independent check on the correctness of the computer program, and also gives some idea of the errors arising from discrete time and horizontal space steps. The results of one comparison are shown in Table I. The following parameter values were used: layer thicknesses 12 m each, relative velocity 0.2 km h^{-1}, diffusion rate 2 m^2 h^{-1}, initially all the dye concentrated in one 0.4 km box in the top layer. The horizontal cell size was 0.4 km, the time step 2 hours. The model was run for 4 days, printing the variance every 6 hours. For a velocity 2v and an exchange rate k (k is the fraction of the layers exchanged per unit time: = diffusion rate/(layer thickness)^2) the theoretical formula for the variance is

$$\sigma^2 = \frac{v^2}{k^2} \quad \tanh kt\,(kt - \tanh kt) + 0.013$$

Table 1

Comparison of dye mixing theory and model

	Variance (km^2)		
Time (h)	Theory	Model	'Corrected' theory
0	0.013	0.013	0.013
6	0.014	0.014	0;014
12	0.026	0.027	0.027
18	0.078	0.081	0.081
24	0.210	0.220	0.221
30	0.474	0.496	0.498
36	0.921	0.962	0.965
42	1.599	1.667	1.670
48	2.547	2.650	2.653
54	3.795	3.935	3.940
60	5.356	5.538	5.542
66	7.236	7.457	7.461
72	9.426	9.682	9.687
78	11.911	12.197	12.202
84	14.670	14.976	14.981
90	17.679	17.993	17.998
96	20.908	21.221	21.225

This is listed in the 'theory' column; the model output is listed in the 'model' column; the agreement is very good. One obvious source of error is the effect of the finite time step in overestimating the vertical mixing rate. In fact, using a time step of 2 hours increases the mixing rate to an effective value of about 2.06 $m^2\ h^{-1}$. The 'corrected theory' column gives the results when this value of mixing rate is used in the theoretical formula; now the agreement with the model is almost too good.

Other time and space steps and other parameter values were tried, all agreeing well with theoretical predictions. We confirmed, for example, that increasing the vertical mixing rate initially increases but later decreases the rate of spreading. The horizontal ring structure sometimes causes problems: eventually the two ends of the dye patch meet instead of spreading out for ever.

These two-layer models concentrate all the shear at one depth. There are also theoretical results for continuous shear (Okubo, 1967) giving a variance formula which is asymptotically valid for large time. In fact, for large time the two-layer theory predicts $\sigma^2 \approx v^2 t/k$ whereas the continuous theory predicts $\sigma^2 \approx 16\ v^2 t/15k$. We have looked at one three-layer run, which should be a better approximation to the continuous — the slope is indeed steeper, but it has not been possible to estimate the slope of the asymptote, because of the ring problem.

There is no real difference at the computational level between steady and oscillating shears; so, we can expect the model to give just as accurate answers for oscillating shear.

We said earlier that a variety of values of box size and time step had been tried, and that the choice did not affect the answer very much. However, all our choices have had the property that adjacent layers have a relative motion of one box length (to within a factor of three or so) in one time step. We can foresee problems arising if the relative motion differs from one box length by a large factor. At one extreme, we might have adjacent layers staggered by half a box length and hardly moving. The mechanism of splitting columns for vertical exchanges would then give rise to a completely spurious horizontal spread, as shown in Figure 1.

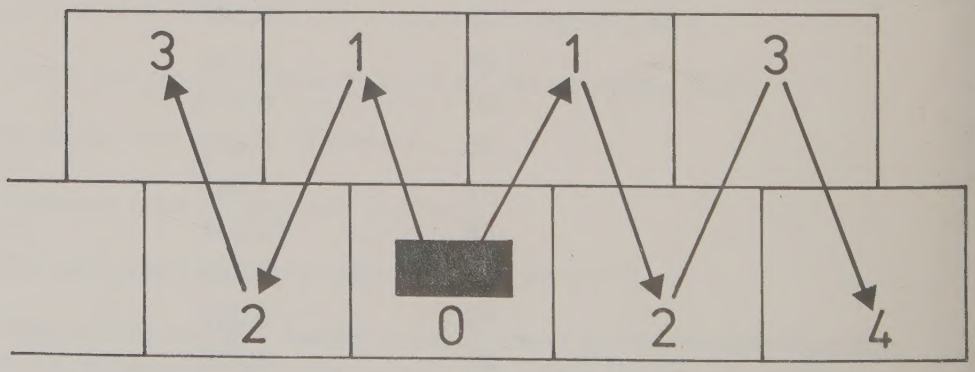

Figure 1. Spurious horizontal diffusion.
In this figure the layers are at rest. A patch of dye initially concentrated in the box labelled O will be spread by vertical mixing into the boxes labelled 1 during the first time step, and thence into the boxes labelled 2 during the second, and so on. In this way the patch will be spread horizontally even though there is no velocity shear.

(This problem is avoided if we change the program to exchange in whole, skew vertical columns.) At the other extreme, if we jump over several boxes in one time step, one box will receive material which should have been spread over several. Something of the sort happens with herbivore migration, where the problem is not the time step but the fact that the animals move only twice a day.

Column runs

Runs of a single column should be able to generate the main feature expected of the simpler "smooth world" theories (Riley, 1963; Steele, 1974) such as the succession of maxima for nutrients, phytoplankton and zooplankton. Further, the vertical distribution should give a midwater chlorophyll maximum following the ideas of Steele and Yentsch (1960).

A major possibility is that with certain functional forms, or values for the coefficients, the system after the "spring outburst" may not go to a steady state but display cyclical behaviour. This might then appear as spatial waves in the full, shear, system.

Table II

Parameters for a standard column run

No. of Boxes	Box Size	Time Step	Running Time	Print Step
1	1.000	4.0	2400.0	48.0

	Top	Mid	Bot
Photosyn rates	0.012	0.010	0.006
Phot Half-sat	1.00		
Plant resp	0.0020		

	Naup	Cop'ite	Adult
Animal weight	0.0100	0.1000	1.0000
Grazing rate	0.0012	0.0054	0.0250
Daily ration	0.030	0.050	0.100
Threshold	0.5000	0.5000	0.5000
Graz half-sat	1,0000	1.0000	1.0000
Growth fraction	0.3000	0.3000	0.3000
Sol Excret Frac	0.3000	0.3000	0.3000
Predation rate	0.0010	0.0010	0.0010
Migration: ZMA	0.5000	0.5000	0.5000
Uptime	0.0	0.0	4.0
Downtm	0.0	16.0	16.0

	Top	Mid	Bot
Layer thicknesses	10.0	10.0	20.0
Diffusion	5.00	0.30	0.30
Max Plant sinking	0.0800		
Deep water nutr	10.0000		

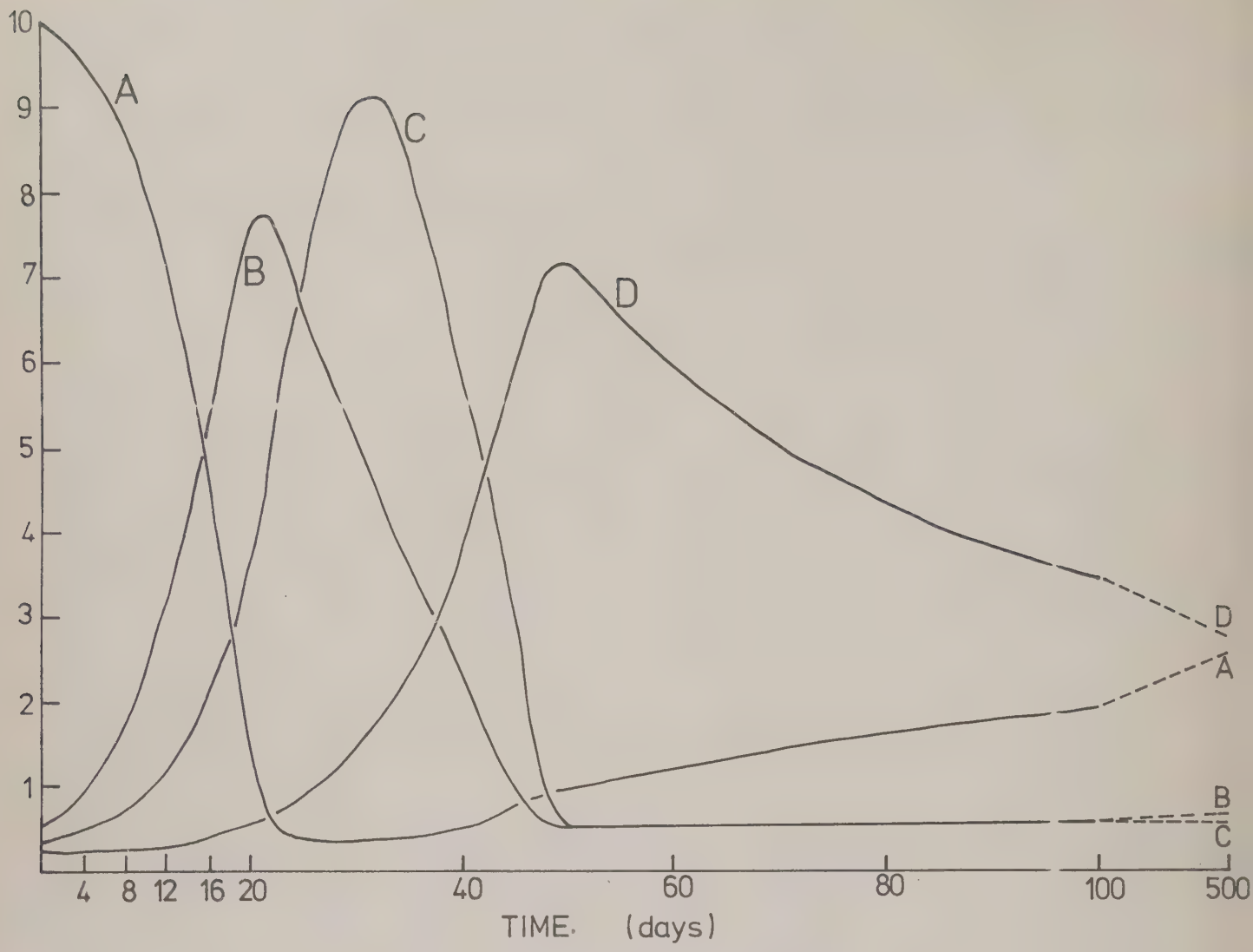

Figure 2. Selected output from a 'standard' column run.
A: surface nutrients, mM N m^{-3}
B: surface phytoplankton mM N m^{-3}
C: thermocline phytoplankton mM N m^{-3}
D: vertically integrated herbivore biomass (mM N m^{-2}) x 10

Table II and Figure 2 give parameters and graphs of selected output for one run, which has been used as a standard for comparison with several other parameter sets. Initial conditions were chosen to represent the start of the spring bloom, and the run reproduces the gross features of the bloom, although herbivore growth is perhaps unrealistically slow, and the adult population falls too much (20%) in the first ten days.

Small (factor of 2) changes in various parameters do not alter the behaviour much. We find in general that the peak phytoplankton is determined by the amount of nutrient, the equilibrium phytoplankton is determined by the threshold, and the other equilibria are largely determined by mixing and predation rates. No systematic study was done.

A series of runs with much higher biological rates produced a much quicker progression through peak to equilibrium (Figure 3). A combination of low photosynthetic rate in the thermocline (greater light attenuation).
and the same leisurely sinking rate meant that there was never a midwater chlorophyll peak. Lowering the photosynthetic rate reduced the phytoplankton peak and increased the equilibrium nutrient concentration, but did not change the equilibrium phytoplankton much — indeed for the upper two layers it was increased. This re-emphasises the importance of the

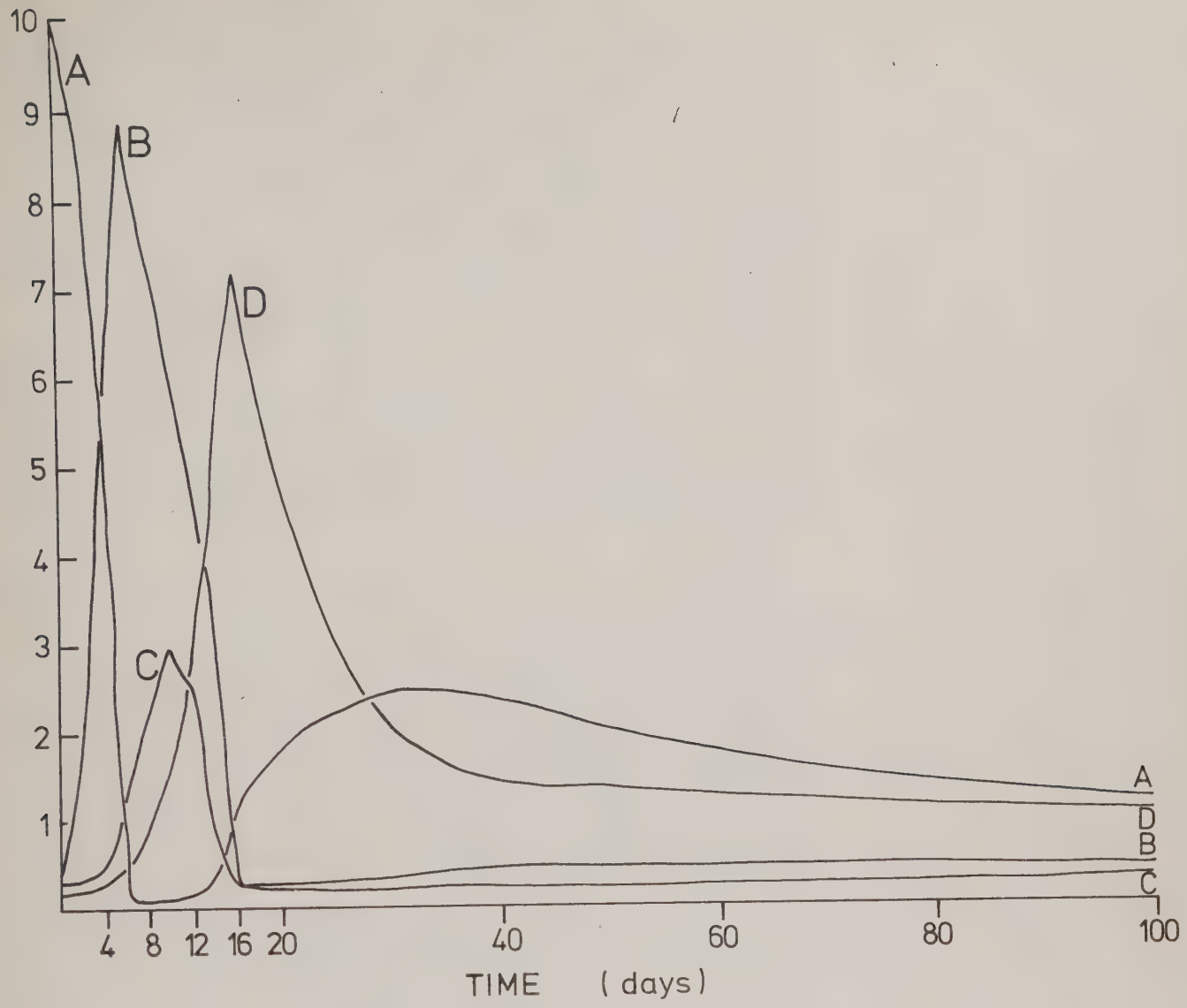

Figure 3. Selected output from a column run with faster biological rates. See Figure 2 for explanation.

threshold. Decreasing the grazing rate as well led to large (though damped) oscillations: possibly there is a limit cycle lurking nearby. Shifting the predation pattern, more on nauplii, less on adults, reduced the oscillations.

The full model

Early runs of the full model showed up an intriguing mechanism in which vertical shear interacts with vertical migration to produce patches of herbivores. Consider two adjacent boxes in an upper layer moving over the deep layer, and suppose that the downstream box has a greater plant concentration. This could mean that during one time step the downstream animal population reaches its ration and descends, while the upstream animal population does not reach its ration until the next time step, when it has moved further downstream, and descends into the same deep box as the previous lot of animals. This effect, gathering herbivores from a wide area into a patch, can be seen in all the full runs.

At the same time, it gives us a computational problem. Because of low computer speed it has not been feasible to use a time step of less than 4 hours. This means effectively that for the adults the ration effect can occur at 8 hours after ascent or not at all (adults descend anyway after 12 hours): an infinitesimal difference in food can make a 4-hour difference in behaviour. Therefore, until it has been possible to do some runs with a smaller time step, these results (and especially spectra taken from them) should be treated with suspicion.

The main approach to the full model was to use pre-outburst conditions everywhere but to vary the plant concentrations slightly (between 0.3 and 0.7 mM N m^{-3}) in some pattern like sin 1/x which has waves of various lengths in it. The range of wavelengths has been extended by considering the same initial conditions with boxes of various lengths. Figures 4 and 5 summarize what happens: oscillations of wavelength less than 10 km are damped quickly, larger ones survive or grow for a while; the ration effect introduces new oscillations which undergo the same process. The parameters here are nearly the same as in Table I — only the upper diffusion is changed, to 10 m^2 h^{-1}. There is a 12½ hour velocity oscillation, with maximum speed 0.8 km h^{-1} in the top layer, 0.4 in the mid.

One of the problems associated with the full model is the volume of its output. Various graphs of the raw data can be useful; another technique which we have begun to explore is the calculation of Fourier components or power spectra of the space sections of different parameters. Fourier analysis is particularly attractive because the answers are constrained to be periodic by the model structure.

Spectral work with initial conditions of the sin 1/x type produced some encouraging results and some problems. The results are presented in Figures 6 and 7: these are graphs of Fourier amplitudes rather than power spectra. They show the fall off in high frequencies, and tend to show that the spectrum is a real part of the ecosystem, as suggested by Platt & Denman (1975), in the sense that the time evolution of the spectrum seems largely independent of its realization. The graphs for each day are from three sets of initial conditions, all of which had the same Fourier amplitudes. The break-up of the herbivore spectrum on day 10 may be a result of the 4-hour time step as discussed earlier.

These results, for a 64 km ring, look plausible, but there are anomalies in comparing it with a 128 km ring — the behaviour of a wavelength appears to depend more on what fraction it is of the whole length than on how long it is. There are difficulties of interpretation: it is not obvious what comparable spectra for 128 and 64 km are. Also there is sure to be interference between wavelengths, since we are dealing with highly non-linear equations. This subject needs much more work.

Discussion

Although a systematic study of the model has barely started, we can draw some tentative conclusions. Most important, we have shown that vertical shear in horizontal currents can play a major role in determining the horizontal distribution of plankton. We have identified a mechanism in which vertical shear and vertical zooplankton migration patterns combine to produce zooplankton patches which neither process could produce by itself.

At the same time we have confirmed that the behaviour of a food chain model is greatly influenced by its closure terms: mixing of nutrients from below at the bottom end, and predation on herbivores at the top. The former shows the need to model the physics of vertical mixing explicitly; the latter suggests that we should look at the effect of different predation functions, even if we do not model the carnivore level. For example, it is possible that a quadratic predation term could combine with different diffusion rates for plants and animals to produce patches as dissipative structures (Segel and Jackson, 1972; Okubo, 1974).

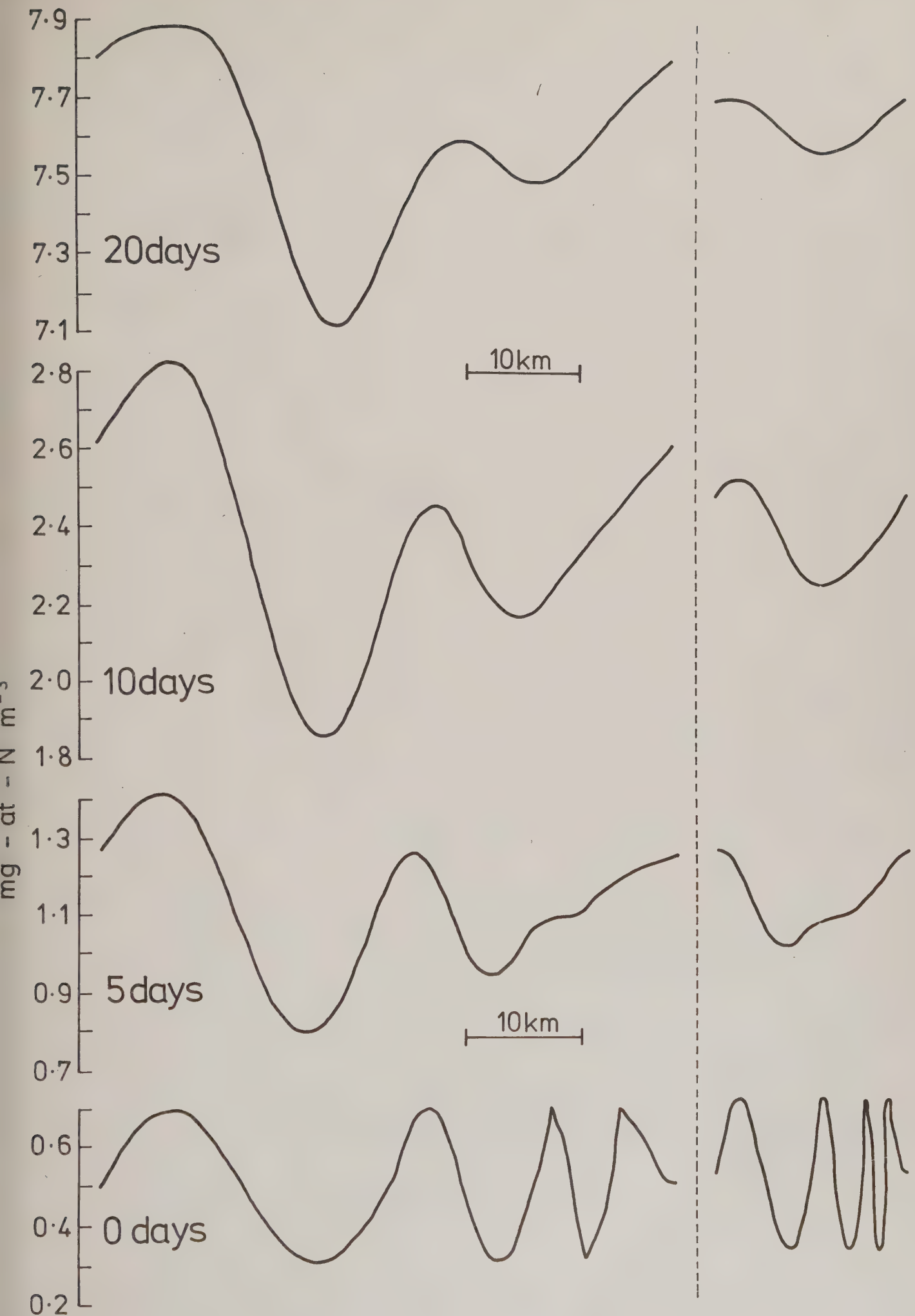

Figure 4. Surface phytoplankton distributions from two full model runs.

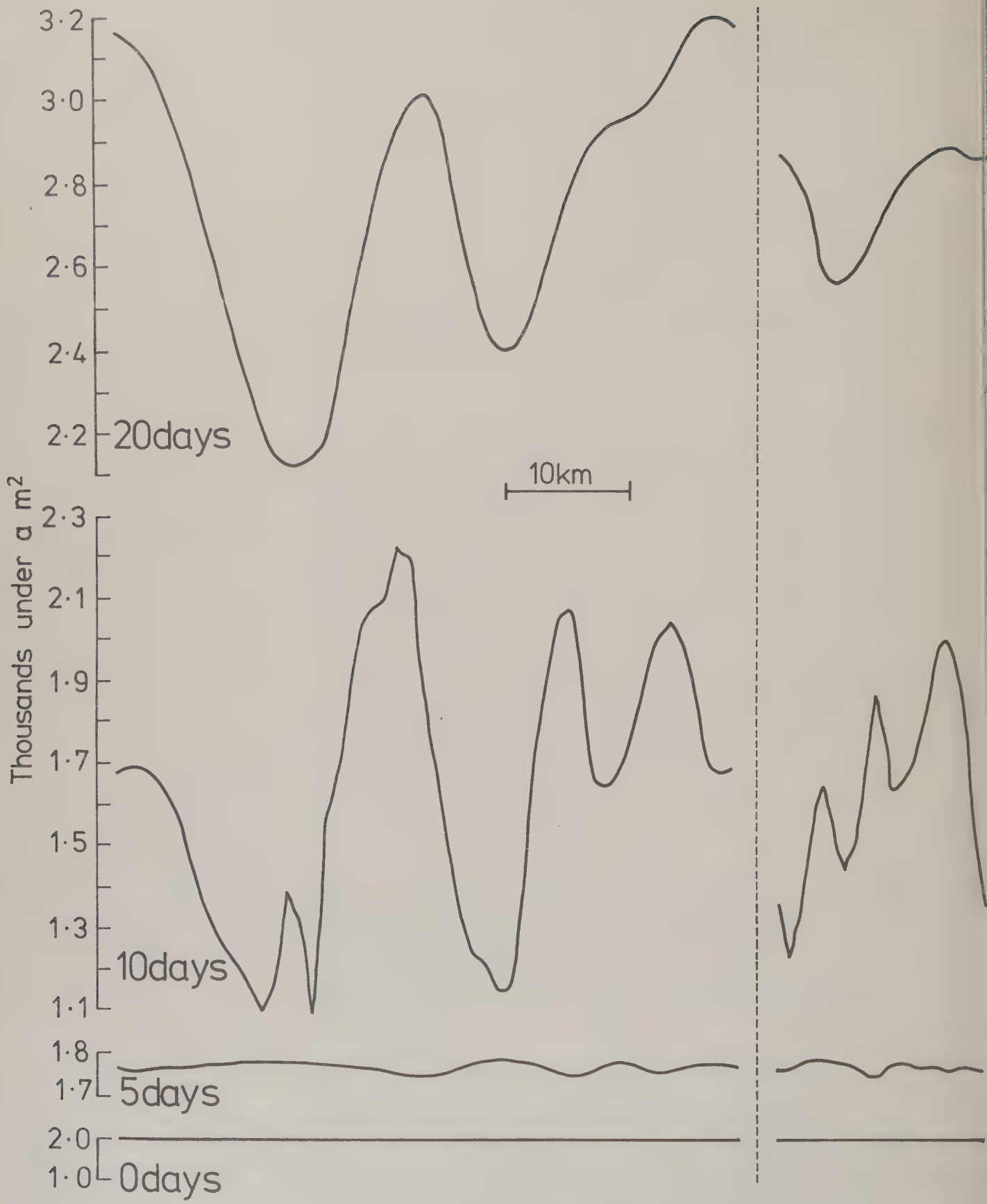

Figure 5. Adult herbivore distributions from the same runs as Figure 4.

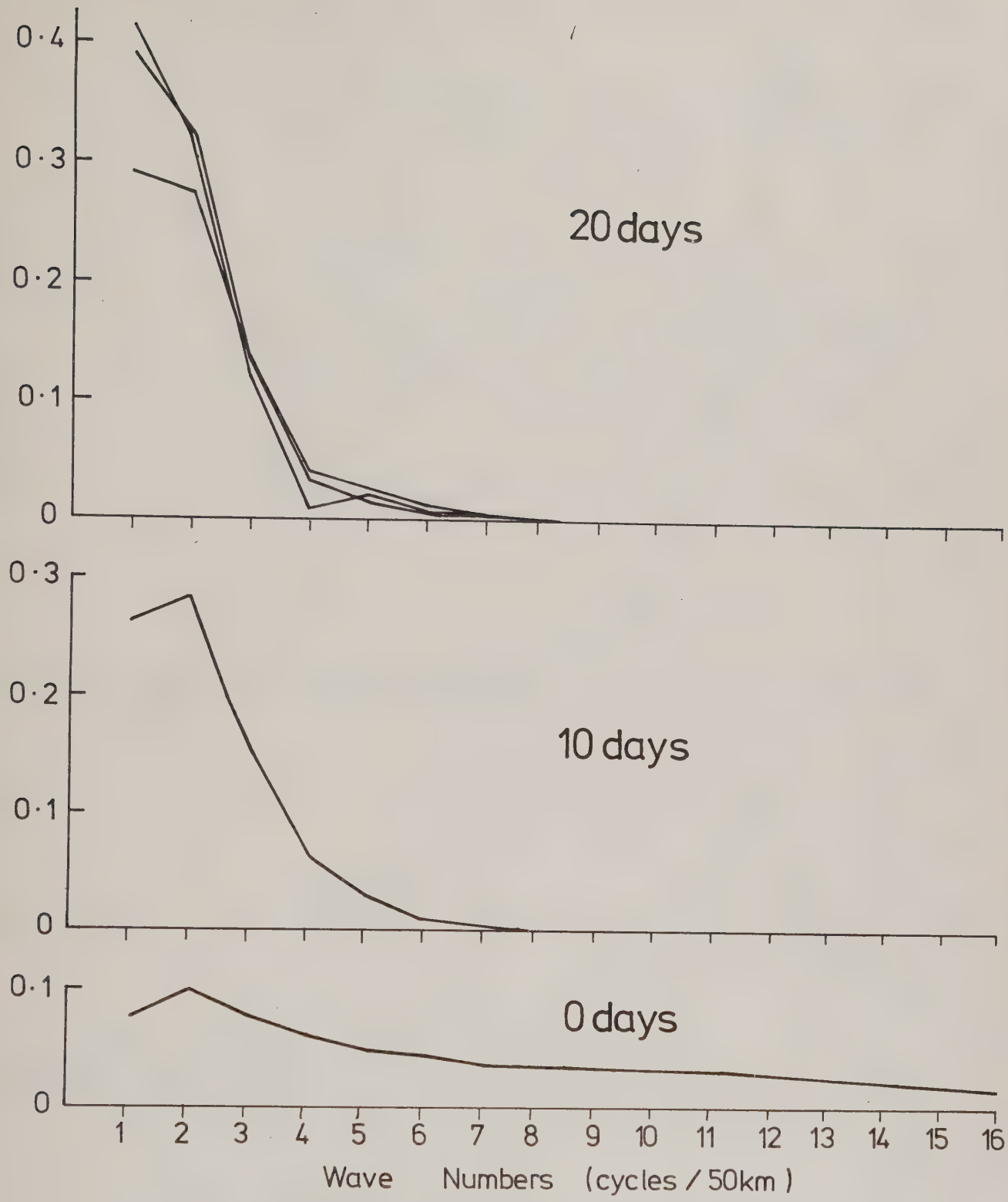

Figure 6. The development of Fourier amplitudes of surface phytoplankton distributions in three full model runs whose initial Fourier amplitudes were identical (arbitrary units). The 50 km run in Figure 4 shows the development of the physical distribution for one of these runs.

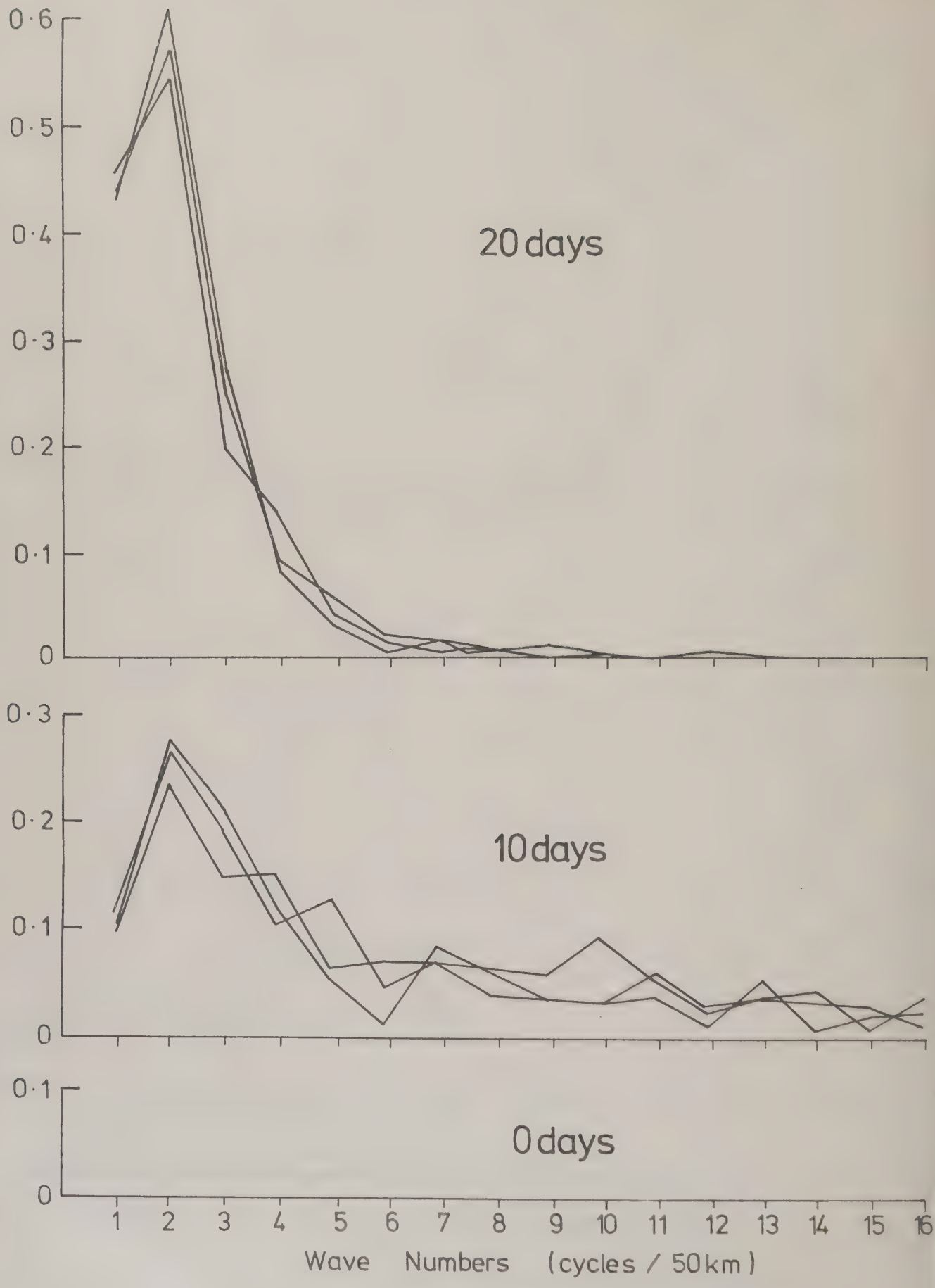

Figure 7. The development of adult herbivore distributions corresponding to Figure 6. See Figure 5 for one of the physical distributions.

In our model, the vertical mixing rate is constant in time and horizontal space. In the sea the rate will be variable, and this will have a great effect on the formation of phytoplankton patches. This confirms the importance of modelling vertical mixing.

We have ignored internal waves, although we realise that they are likely to be important both in the formation of patches and in the interpretation of observations made at sea (Kamykowski, 1974, 1976; Denman, 1976). We have no plans at the moment to model them.

Summary

We have constructed a mathematical model of the ways in which vertical processes such as turbulent mixing and zooplankton migration can affect the horizontal distribution of plankton. The model simulates shear-induced diffusion well, and its simulation of the biology is plausible. We have discovered an unexpected process in which vertical current shear can combine with vertical migration to produce zooplankton patches.

The model shows that vertical interactions can be an important component in determining the horizontal distribution of plankton, and that they merit further study.

References

Bowles, P., Burns, R., Hudswell, F. and Whipple, R. 1958. Sea disposal of low activity effluent. United Nations International Conference on the Peaceful Uses of Atomic Energy, *2nd Geneva, 1958.* Proceedings, vol. **18.** New York, U.N., 376-389.

Conover, R.J. 1968. Zooplankton – life in a nutritionally dilute environment. *Am. Zoologist* **8,** 107-118.

Denman, K.L. 1976. Covariability of chlorophyll and temperature in the sea. *Deep-sea Res.* **23,** 539-550.

Dugdale, R.C. 1977. Nutrient Modelling. *E.D. Goldberg et al. eds. The Sea,* vol. 6. New York, Wiley, 789-806.

Eppley, R.W., Holmes, R.W. and Strickland, J.D.H. 1967. Sinking rates of marine phytoplankton measured with a fluorometer. *J. Exp. Mar. Biol. Ecol.* **1,** 191-208.

Evans, G.T. 1977. A two-layer shear diffusion model. *Deep-Sea. Res.* (in press).

Kamykowski, D. 1974. Possible interactions between phytoplankton and semidiurnal internal tides. *J. Mar. Res.* **32,** 67-89.

Kamykowski, D. 1976. Possible interactions between plankton and semidiurnal internal tides. II. Deep thermoclines and trophic effects. *J. Mar. Res.* **34,** 499-509.

Kierstead, H. and Slobodkin, L.B., 1953. The size of water masses containing plankton blooms. *J. Mar. Res.* **12,** 141-147.

Kullenberg, G.E.B. 1974. An experimental and theoretical investigation of the turbulent diffusion in the upper layers of the sea. Univ. of Copenhagen, Inst. of Phys. Oceanogr., Rep. No. 25. pp. 212.

Landry, M.S. 1976. The structure of marine ecosystems: an alternative. *Mar. Biol.* **35,** 1-7.

Longhurst, A.R. 1976. Vertical migration. *Cushing, D.H. and Walsh, J.J. eds. The Ecology of the Seas.* Oxford, London, Edinburgh, Melbourne, Blackwell Scientific Publications, 116-137.

Mackas, D. and Bohrer, R. 1976. Fluorescence analysis of zooplankton gut contents and an investigation of diel feeding patterns. *J. Exp. Mar. Biol. Ecol.* **25,** 77-85.

Okubo, A. 1967. The effect of shear in an oscillatory current on horizontal diffusion from an instantaneous source. *Int. J. Oceanol. and Limnol.* **1,** 194-204.

Okubo, A. 1971. Oceanic Diffusion Diagrams. *Deep-Sea Res.* **18,** 789-802.

Okubo, A. 1974. Diffusion-induced instability in model ecosystems. Chesapeake Bay Institute, Tech. Rpt. 86. pp. 17.

Pearre, S. 1973. Vertical migration and feeding in *Sagitta elegans* Verrill. *Ecology* **54,** 300-314.

Platt, T. and Denman, K.L. 1975. Spectral Analysis in Ecology. *Ann. Rev. Ecol. & Syst.* **6,** 189-210.

Raymont, J.E.G. 1963. Plankton and productivity in the oceans. New York Macmillan, 660 pp.

Riley, G.A. 1963. Theory of food-chain relations in the ocean. *Mill, M.N. e The Sea, vol. 2.* New York. Wiley, 438-463.

Riley, G.A. 1976. A model of plankton patchiness. Limnol. and Oceanogr. **21,** (6), 873-879.

Segel, L.A. and Jackson, J.L. 1972. Dissipative structure: an explanation and an ecological example. J. Theor. Biol. **37,** 545-559.

Skellam, J.G. 1951. Random dispersal in theoretical populations. Biometrika, **38,** 196-218.

Steele, J.H. 1974. The Structure of Marine Ecosystems. Cambridge, Mass., Harvard Univ. Press. 128 pp.

Steele, J.H. 1976. The role of predation in ecosystem models. Mar. Biol. **35,** 9-11.

Steele, J.H. and Frost, B.W. 1977. The structure of plankton communities. Phil. Trans. R. Soc. (in press).

Steele, J.H. and Yentsch, C.S. 1960. The vertical distribution of chlorophyll. J. mar. Biol. Ass. U.K. **39**(2), 217-226.

Sverdrup, H.U. 1953. On the conditions for the vernal blooming of phytoplankton. J. Cons. Explor. Mer **18,** 287-295.

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